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Original article

The relationship between phenological traits and brood size of the white stork *Ciconia ciconia* in western Poland

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ABSTRACT

Changes in the spring arrival dates of migrant birds have been reported from a range of locations and many authors have focused on long-term trends and their relationship to temperature and other climatic events. However, there may be consequences (costs) for changes in arrival dates which long-lived birds may have to repay in the future. In this paper we take the opportunity provided by a detailed monitoring scheme to examine several features of the timing of arrival in relation to chick production of white storks *Ciconia ciconia* in Poland during the period 1983–2003. Longer occupied nests were associated with greater productivity than shorter occupied ones. Early arriving pairs were more productive than later ones. Individual birds and the whole population could achieve greater productivity by earlier arrival. However, high chick production in one year tended to be followed by a slightly lower productivity and delayed arrival in the following year. Hence, the cost of early arrival at breeding sites may have to be paid for in the following, rather than in the current, year.

1. Introduction

In migratory birds, the earliest individuals to arrive on their breeding grounds typically occupy the best territories and consequently have the highest reproductive success (Potti, 1998; Kokko, 1999; Forstmeier, 2002). Moreover, in some species, such as the white stork *Ciconia ciconia* which builds large, ''perennial'' nests and where the number of potential nest sites is sometimes limited (e.g. Creutz, 1985; Profus, 1991), advanced arrival increases the opportunities to maintain occupation of good nests and save the energy needed for nest construction. Early arrival also provides the opportunity for an earlier start to egg laying (Møller, 1994; Brown and Brown, 2000; but see Both and Visser, 2001), which strongly influences breeding capacity. Therefore, a strong selection is expected for early arrivals from wintering grounds located in tropical Africa (see Kokko, 1999; Morbey and Ydenberg, 2001 for more general models). This view is supported by changes in recent decades, when migratory birds have tended to return earlier from wintering grounds to breeding places as a consequence of climate change (reviews in: Walther et al., 2002; Parmesan and Yohe, 2003; Lehikoinen et al., 2004). This tendency has also been noted in the white stork (Ptaszyk et al., 2003; Tryjanowski et al., 2004). Moreover, previous papers have clearly indicated a link between arrival date and timing of breeding (Tryjanowski et al., 2004), suggesting a strong evolutionary pressure on earlier migration.

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On the other hand, birds that arrive early on their breeding grounds can suffer the consequences, and in extreme cases, death (Whitmore et al., 1977; Brown and Brown, 2000), mainly due to the influence of and/or changes in the food supply. It can be argued that the costs of early arrival would always be greater for individuals in poorer condition (Møller, 1994; Kokko, 1999; Forstmeier, 2002). However, to date, such results have only been presented for relatively short-lived passerines. The situation for long-lived species may differ for a number of reasons. Firstly, one poor year of reproductive output following adverse weather on the breeding grounds (Tryjanowski et al., 2004) may not be too detrimental to lifetime reproductive success. Secondly, the cost of reproduction in long-lived species may result in a reduction in future fecundity, rather than reduced survival (Linden and Møller, 1989; Hanssen et al., 2005).

In this study we start to answer the classical questions on the relationship between arrival date and chick production. Secondly, we examine how arrival date and productivity are linked to particular nest sites and if any pattern is discernible between years. Finally, to the best of our knowledge for the first time in phenological studies, we try to show the potential cost to the females of early arrival on the breeding grounds and how it affects their potential reproductive performance. From earlier work, we anticipated a negative relationship between arrival date and the number of chicks fledged in a particular year (Tryjanowski et al., 2004). We also anticipate that, for a long-lived species like the white stork, early arrival and greater chick productivity may result in higher reproductive costs although the consequences for the population may be delayed (Hanssen et al., 2005; Sæther et al., 2005).

2. Study area and methods

The study was conducted during 1983–2003 in the agricultural landscape of western Poland, near Poznań (52° N, 16° E). In this area of 1227 km^2, arable fields are interspersed with meadows, pasture, human settlements and small woods. In the study area white storks build nests mainly on the roofs of farm buildings, on electricity poles and in trees, thus making the nests extremely conspicuous; they are also used year after year. A total of 98 nests were monitored in the area. The large obvious nests of the white stork are associated with human settlements and it is highly unlikely that any nests were missed. The dates of arrival of white storks to their nests were recorded on special forms by farmers living near occupied nests and sent direct to the authors (details in Ptaszyk et al., 2003). In the field information on the timing of both partners returning to a nest was collected although in this paper we concentrate on the date of arrival of the second partner (mostly females—Creutz, 1985; Tryjanowski et al., 2004), assuming that the decision on the timing of breeding is more influenced by the female. Breeding success was determined by researchers counting the numbers of chicks present in the nest in July (Tryjanowski et al., 2004).

Throughout this paper we focus on individual nests rather than individual birds. However, ringing recoveries in the studied population revealed no change in breeding locations in females (Chernetsov et al., 2006), which suggests that over their lifetime the female will breed in a single nest. Therefore, with some caution, the data can be interpreted as representative not only of the nest, but also for individual females as well.

Arrival dates of the second bird of a pair (AD2) were converted to days post December 31 prior to analysis. The number of years that a nest was occupied, the mean AD2 and the mean number of chicks produced was calculated across the study period.

In this paper we examine patterns between arrival and brood size and the relationship with the following year. We use a range of regression and correlation techniques, weighted by the number of records where stated.

Throughout the text, values are reported as means ± SE. Analyses were conducted using the Minitab v.13 (www.minitab.com) statistical package. All basic statistical analyses were applied according to the recommendations of Zar (1999).

3. Results

In the years 1983–2003 a total of 1267 nesting attempts were recorded from the 98 nest sites; an average of 12.9 years of data per nest. The mean number of chicks was 1.68 ± 0.08. AD2 information was available for 593 (47%) of these nesting attempts.

3.1. *Relationship between arrival and productivity*

Early nests were more productive. For the 91 nests for which AD2 data were available there was a significant negative relationship between mean number of chicks and mean AD2 (Fig. 1, regression weighted by number of years in mean: $b = -0.053 \pm 0.011$, $F_{1,89} = 22.09$, $R^2 = 19.9\%$, $P < 0.001$). This coefficient suggests that nests with a mean AD2 19 days earlier would have a one chick increase in mean productivity. There was a significant positive correlation between mean

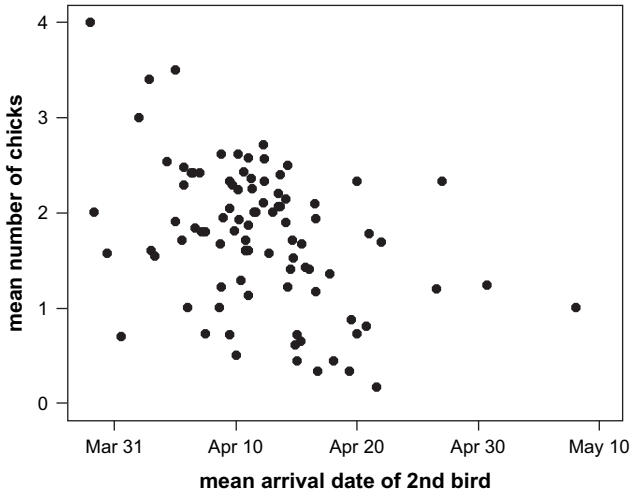

Fig. 1 – Relationship between mean arrival date of the 2nd bird of each pair and mean number of chicks produced from 91 nests in western Poland between 1983 and 2003.

chick number and the numbers of years the nest was occupied in the 1983–2003 period ($r = 0.27$, $P = 0.007$) such that longer occupation was associated with higher chick production. No significant relationship existed between mean AD2 and the number of years a nest was occupied ($r = -0.15$, $P = 0.16$).

Chick production was higher in years of early arrival and, when considered as annual means, a similar relationship existed between chick numbers and arrival date (regression weighted by number of nests in mean: $b = -0.059 \pm 0.015$, $F_{1,19} = 15.70$, $R^2 = 45.3\%$, $P = 0.001$).

3.2. *Patterns within individual nests*

On 425 occasions the change in chick numbers and the change in AD2 could be compared between year n and year $n + 1$. The correlation between the two ($r = -0.18$) is highly significant ($P < 0.001$), implying that earlier arrival at a nest in the following year was associated with greater chick production (Fig. 2). Also apparent was that high production in the current year was followed by later arrival in the following year (Fig. 3; $r = 0.13$, $P = 0.006$).

For 56 nests it was possible to separately regress AD2 in year $n + 1$ on that in year n. The mean slope, -0.122 ± 0.077, was not significantly different from zero ($t_{55} = -1.58$, $P = 0.12$) and did not allow us to reach any conclusions about change in AD2. However the regressions of chick numbers in year $n + 1$ on those in year n separately for 94 nests produced a mean slope of 0.139 ± 0.040 ($t_{93} = 3.48$, $P = 0.001$), suggesting that high chick numbers in one year were followed by lower numbers the following year and vice-versa.

To investigate more fully the change from one year to the next we examined the chick numbers from the 17 nests recorded throughout the 21-year study. A turning point test (Kendall, 1973) can be applied to determine whether the number of changes from one year to the next is random with expected mean $2/3(n - 2)$, i.e. 12.67. The 17 nests produced between 12 and 18 turning points with a mean of 14.82 ± 0.47. This was significantly greater than expected using a one tailed t-test $t_{16} = 4.15$, $P < 0.001$. This further suggests that high productivity one year was followed by lower productivity the next and vice versa.

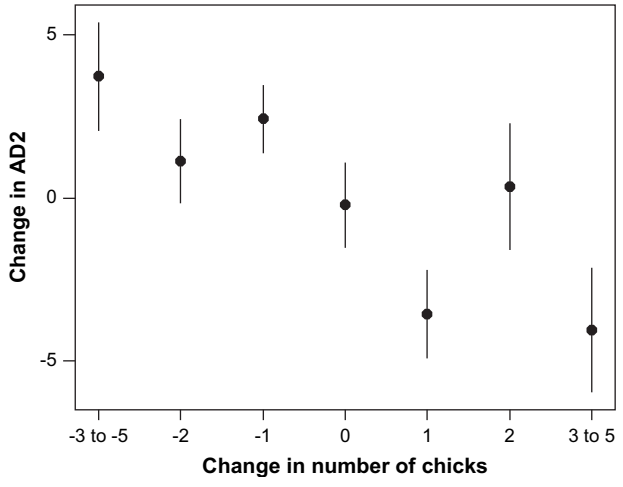

Fig. 2 – The relationship between mean change ± SE in the arrival date of the 2nd bird between year n and year $n + 1$ and the change in chick number between year n and year $n + 1$. Negative change figures in AD2 indicate earlier arrival, positive value in change in chick numbers indicate greater production.

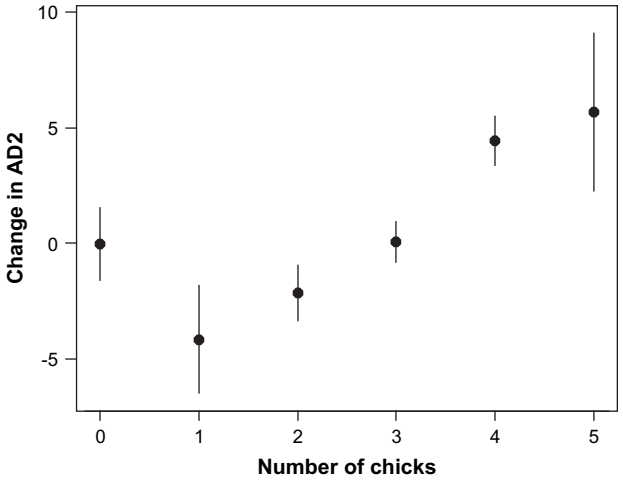

Fig. 3 – The relationship between mean ± SE change in the arrival date of the 2nd bird between year n and year $n + 1$ and chick numbers in year n. Negative change figures in AD2 indicate earlier arrival.

4. Discussion

We found a negative relationship between arrival timing and the number of reared chicks, which confirms our previous results (Kosicki et al., 2004; Tryjanowski et al., 2004) that early arrival to breeding grounds, as in many other animals (review in: Svensson, 1997; Morbey and Ydenberg, 2001), has advantages for the white stork. We think this is the consequence of two factors. Firstly, individuals in better condition arrived earlier and, secondly, early birds re-occupied better nests located in better territories (Tryjanowski et al., 2005). Interestingly, the relationship between arrival date and productivity is repeatable over years, which suggests that early arrival is always profitable. This suggests that the costs of an early return to breeding grounds have been relatively low in the study period or have been masked by large profits (see also Tryjanowski et al., 2004). We suspect that this should lead to direct and/or indirect selection for early arrival.

Although arrival timing to individual nests is significantly repeatable between years, we also found differences in arrival dates between years. To date, arrival date differences between years have been linked to weather conditions (Tryjanowski et al., 2002; Ptaszyk et al., 2003) and/or nest quality (Tryjanowski et al., 2005) or just to the individual traits of a particular nest/pair (this study). However, it may also be related, as we suggest in this paper, to levels of reproduction in the previous year. Therefore early migration and reproductive output may both affect future reproduction. As in other long-lived species (Drent et al., 2003; Bêty et al., 2004; Hanssen et al., 2005) they may pay the costs of high

reproductive output in following years, and too early an arrival may thus indirectly result in a future lower reproductive rate. We predict that cost limited reproduction rate in the future may be an important selective constraint on the migratory pattern (and even, in consequence, sedentary tendency) in the white stork, as well as in many other long-lived large migratory species.

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